Metabolic Ecology

Scaling refers to the effects or consequences of a change in size (Schmidt-Nielsen 1975); thus, biological allometric scaling refers to how a change in size affects rates of biological structures and processes (West et al. 1997). These relationships are described by allometric equations of the form: $Y = Y_0 M^b$, where Y is the dependent biological variable (e.g. mass-specific basal metabolic rate), $Y_0$ is a normalization constant characteristic of the organism, M is body size, and b is the allometric exponent (Huxley 1932). It is suggested that Galileo Galilei (1637) was the first scientist to publish work on scaling when he explored the size and strength of bones necessary to support large mammals such as elephants (Schmidt-Nielsen 1975). Numerous biological variables have since been found to scale predictably with body size. For example, Sarrus and Rameaux (1839) recognized that metabolism is limited by the ability to offload heat, and thus is proportional to surface area. Rubner (1883) proposed that metabolism should scale with body mass raised to the power of 2/3, and this allometric exponent was later changed to 3/4 by Kleiber (1932) (Hoppeler and Weibel 2005).

Although contested, most allometric exponents have been found to be multiples of ¼; for example, whole organism metabolism scales as $M^{¾}$, cellular metabolism and maximal population growth scale scale as $M^{-¼}$, and embryonic growth and development scale as $M^{¼}$ (West et al. 1997). Theoretical scientists have proposed several hypotheses to explain these patterns, including elastic similarity/buckling of terrestrial organisms (McMahon 1975), diffusion across hydrodynamic boundaries in aquatic organisms (Patterson 1992), and fractal networks of branching tubes (i.e. mammalian vascular network; West et al. 1997; Bejan 2000), where animals are driven not by demand, but supply of energy via the vascular "fuel delivery system" (Hoppeler and Weibel 2005). A more complex model by Darveau et al. (2002) suggests metabolic scaling is driven by an allometric multilevel cascade that controls the energy processes of both supply *and* demand. Meanwhile, experimental scientists have been trying to test the ¾ scaling law with experimental data, but disagree on which metabolic rate to use (e.g. basal, field, maximal).

Although neither theorists nor experimentalists have been able to converge on one metabolic scaling law, this work has laid the foundation for a recent unified approach to biological scaling in which the physical and chemical processes that govern metabolism are combined in a metabolic theory of ecology (Brown et al. 2004). This work extends cell and individual-level metabolic scaling allometries to population, community, and ecosystem levels. For example, species diversity, population density, biomass turnover and energy flux. Because metabolism is the biological processing of energy and materials (stoichiometry), this theory inherently links the matter and energetics models of Reiners (1986). This theory holds that metabolic rate is the most fundamental biological rate and is thus inextricably linked with ecological processes of populations, communities, and ecosystems.

The metabolic theory of ecology has spawned a large field of research designed to test the quantitative predictions that it affords (e.g. Rombouts et al. 2011). Also, given the relationship between metabolism and temperature, it provides a framework for testing the ecological effects of climate change (e.g. Marshall and McQuaid 2011). Scrutiny persists, however (Algar et al. 2007), and it remains to be seen if, as Brown et al. (2004) suggest, "metabolic theory may provide a conceptual foundation for much of ecology, just as genetic theory provides a foundation for much of evolutionary biology"

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